

RATE OF WATER PROPULSION IN MYTILUS CALIFORNIANUS AS A FUNCTION OF LATITUDE

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Although extensive studies have been made on the physiological effects of temperature change in poikilotherms, very seldom has this information been applied to a study of animal activity in relation to latitude. It is common knowledge that a lowering of temperature results in a reduction in metabolism in cold-blooded animals. Consequently, it is classically assumed that marine invertebrates inhabiting the colder waters of the higher latitudes have lower metabolic rates (Wimpenny, 1941).

However, there are many indications in the literature that species living in warmer and in colder latitudes are adapted in some degree to the temperature difference, not only in their tolerable limits but also in activity. For example, Takatsuki (1928) found that a species of oyster from Japan has a higher heart rate at any given temperature than another species from the tropical Pacific. Even within the same species, populations at higher latitudes are more active than those from lower at any temperature between the zones of heat depression and cold depression (Mayer, 1914 on *Aurelia*; Spärck, 1936 on several pelecypods including *Mytilus edulis*; Fox, 1936, 1938, 1939; Fox and Wingfield, 1937 and Wingfield, 1939 on polychaetes, crustacea and other groups). The result appears to be that at their natural temperatures, activity is nearly the same (Thorson, 1946, 1950 on pelecypod respiration and on the duration of larval life).

The review of Bullock (1951) covers the available information relating to temperature compensation in aquatic poikilotherms. Though the fact of the larger size of northern animals was known and the effect of increasing weight on the metabolism per unit weight of the organism was recognized, most of the earlier experimenters did not make quantitative evaluation of these factors in discussing their results. The present investigation is an attempt to understand the effect of temperature on an index of activity, the rate of water propulsion in representatives of a single species, *Mytilus californianus*, with special reference to the latitudinal distribution of the species and under weight controlled conditions. Though it is possible that the latitudinal differences in a species might be due to several factors, such as local nutritional conditions, oxygen and mineral content of the waters, for the present study temperature differences only are experimentally analyzed and correlated with the temperatures of the localities of origin of the animals.

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every aspect of the investigation. To Dr. John L. Roberts for several courtesies extended to me, I am greatly indebted. Thanks are due to other members of the staff of the Zoology Department, for their generous attention to my several needs. Particular mention must be made of the kindness with which Dr. Emery F. Swan sent me mussels and detailed data from Friday Harbor, Washington.

MATERIAL AND METHODS

Mytilus californianus Conrad, collected from Los Angeles (Lat. 34° 00' N), Fort Ross (Lat. 38° 31' N) and Friday Harbor (48° 27' N), were used in the present investigation.² The mussels from the north were transported in moist air in insulated boxes and in both cases were transferred to aquaria of fresh sea water at a temperature chosen to approximate that at which they were collected not later than 48 hours after removal from their natural waters. To correspond with this treatment, local mussels were kept in insulated boxes after collection, for similar lengths of time, before being transferred to aquaria. Throughout the experimental period the mussels were kept at the supposedly natural temperatures which were 16°, 10° and 6.5° C., all $\pm 1.5^\circ$ C., for Los Angeles, Fort Ross and Friday Harbor respectively. Sea water in the aquaria was continually aerated but was not running; it was changed once a week. This effectively eliminated the factor of excessive reduction in the salinity of sea water due to condensation at low temperatures. Over a week the salinity of the sea water in aquaria at 6.5° C. fell from 34.3% to 31.0% in extreme cases. The animals were not obtaining significant quantities of food.

The method described by Jørgensen (1943, 1949) was used for determination of the rate of water propulsion. This method depends on photoelectric estimation of the rate of clearing of suspensions of colloidal graphite. The same batch of graphite (Prodag, particle size 5–15 μ) was used throughout the course of this investigation, although it was observed that the values obtained by using Aquadag (particle size 1–2.5 μ) were not different. Pumping rate was not affected by the concentration of the suspension or its age within the limits used. Pumping rates as measured may not necessarily be equated with feeding rates, but the values obtained showed insignificant variation (see legend, Fig. 3) and correspond well with the values Jørgensen (1949) obtained on *Mytilus edulis* with flagellates and diatoms and which he interpreted as due to normal feeding with a "feeding mucus." The fact that the measured rates are constant for several individuals of any given weight from the same population, at any given temperature, permits of a comparative study. Each individual mussel was experimented upon from three to five times at each temperature, in vessels of 2 to 2.5 liters capacity. Oviparous individuals were eliminated not only because they would effect the weight-specific rates but also because they were erratic in their activity.³

² All the mussels were collected from about 1½ to 2 feet above the 'O' tide level.

³ Since writing the above account, data (to be published later) have been collected, which show that mussels from the low inter-tidal have a faster pumping rate compared to those 4 to 6 feet higher up on the same piling or rock surface. Further, a tidal-rhythmicity of the rate of water propulsion (which persists for over four weeks in the laboratory) in *Mytilus californianus* has been discovered. These two factors account for some of the variation reported above.

RESULTS

Shell-weight as a function of latitude

While readings of weight of soft parts were being taken, it was noticed that the mussels from northern latitudes had relatively smaller percentage of the total weight as soft parts. Within the weight range recorded, shell weight is directly proportional to the wet weight of soft parts at any given latitude (Fig. 1A). The slopes of the lines show a consistent increase with latitude. When the shell weight is expressed as a percentage of total weight and is plotted against latitude (Fig. 1B),

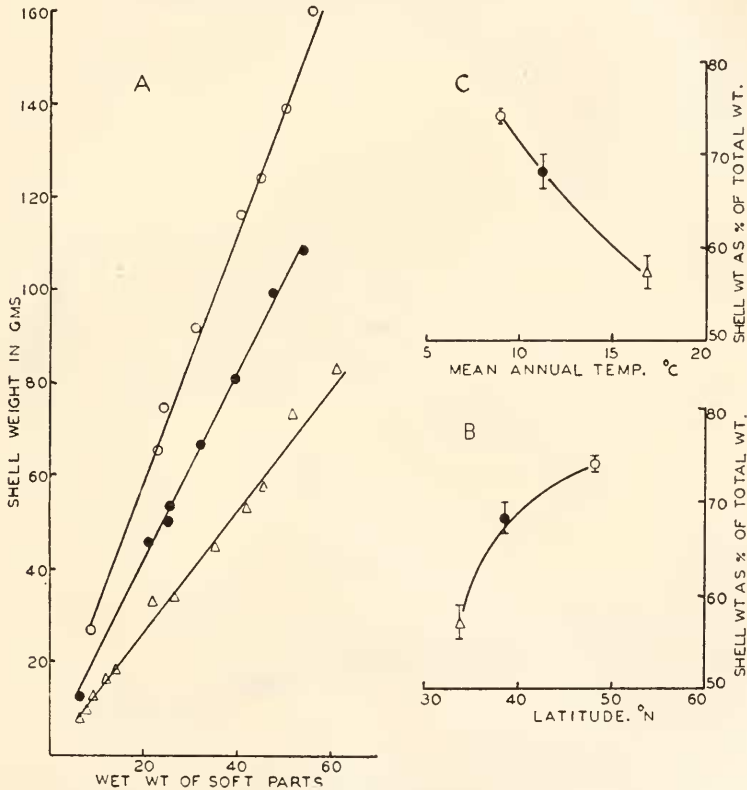


FIGURE 1. Weight of shell as a function of latitude in *Mytilus californianus*. Δ Los Angeles; \bullet Fort Ross; \circ Friday Harbor. Mean annual temperature data from Scripps Institution of Oceanography, La Jolla.

there is an initial rapid increase in the percentage of shell weight, which flattens toward the higher latitudes. But, if the same percentage values of shell weight are plotted against mean annual temperature of the given locality (Fig. 1C), there is a close relation between decrease in temperature and increase in percentage of shell weight. Factors like duration of exposure, crowding and nature of the surface might influence this ratio at local areas. Thus Fox and Coe (1943) obtained a

higher percentage of shell weight for mussels cultured under water without exposure, at La Jolla. These results are exceptions to the common generalization that animals of cold northern latitudes tend to have thinner and more fragile shells (Wimpenny, 1941).

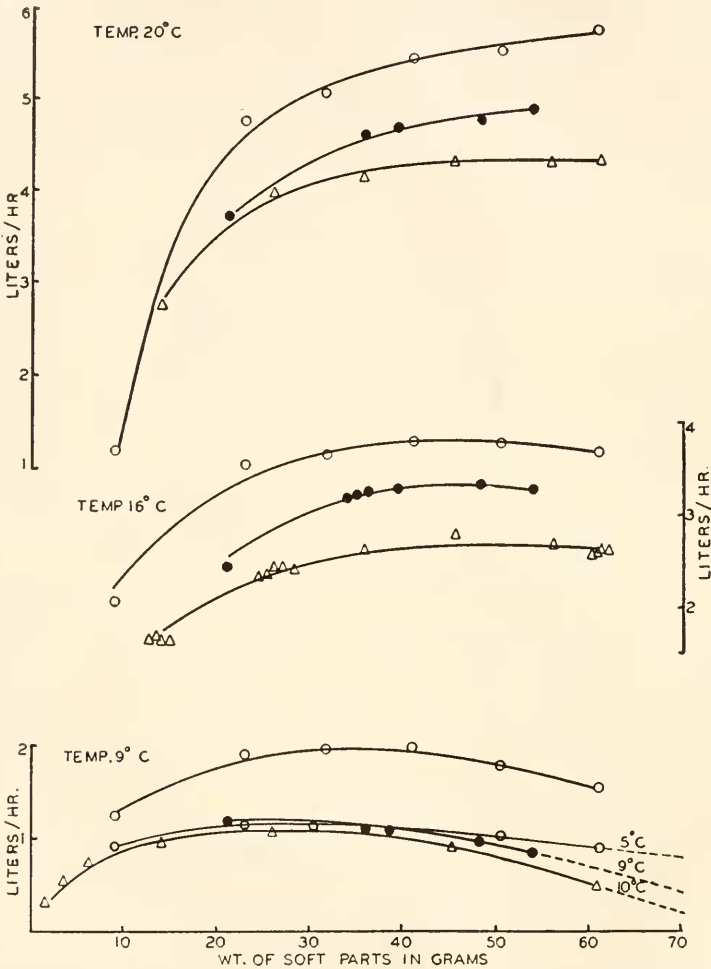


FIGURE 2. Absolute rate of pumping as a function of weight at different temperatures in *Mytilus californianus* from different latitudes. Δ Los Angeles; \bullet Fort Ross; \circ Friday Harbor. Each point represents the average for five to twenty-five readings. Each weight group consisted of three to five mussels. See Figure 3 for statement of variation.

Rate of water propulsion as a function of latitude

A comparison of the effect of temperature on the absolute rate of pumping in animals of increasing weight, from different latitudes (Fig. 2), indicates that at any given temperature animals of equal weight from higher latitudes have a higher total pumping rate than those from more southerly latitudes.

At minimal temperatures (bottom, three curves) the absolute rate of pumping increases with increasing weight, until a certain point and then declines with increasing weight. This decline in absolute pumping rate with increasing weight is slower in higher latitudes. The fact that at their local minimal temperatures the northern animals can grow larger and yet remain as active as a much smaller animal

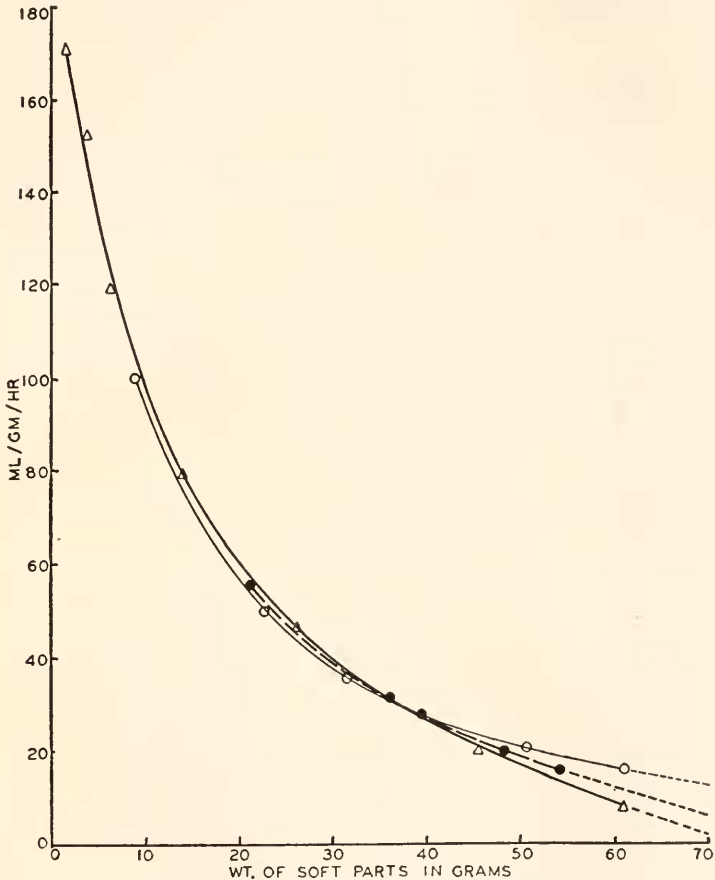


FIGURE 3. Weight-specific rate of pumping of *Mytilus californianus* from different latitudes at approximately minimal temperatures at these latitudes. Δ Los Angeles at 10° C.; \bullet Fort Ross at 9° C.; \circ Friday Harbor at 5° C. Variation of rate in either direction not greater than $\frac{1}{2}\sqrt{n}$, where n is ml./gm./hr.

from a southern locality at its own minimal temperature, correlates well with the known larger size of animals from higher latitudes.

The weight-specific rate of pumping of the mussels from different latitudes appear identical at the minimal temperatures encountered at the respective latitudes (Fig. 3) (according to best available sources—Scripps Institute of Oceanography and U. S. Coast and Geodetic Survey), except that the decline in rate of activity per gram in larger animals is slower in samples from the higher latitudes.

In the cold-adapted, higher latitude animals, the smaller individuals are the first to be affected adversely by high temperatures (Fig. 2, top curve).

Comparing the rate of pumping per unit weight in *Mytilus californianus* of similar weights from different latitudes (Fig. 4), it is evident that at any given temperature animals from the higher latitudes have a much higher rate per unit weight than those from lower latitudes. A 20 gm. animal from either Los Angeles or Fort Ross

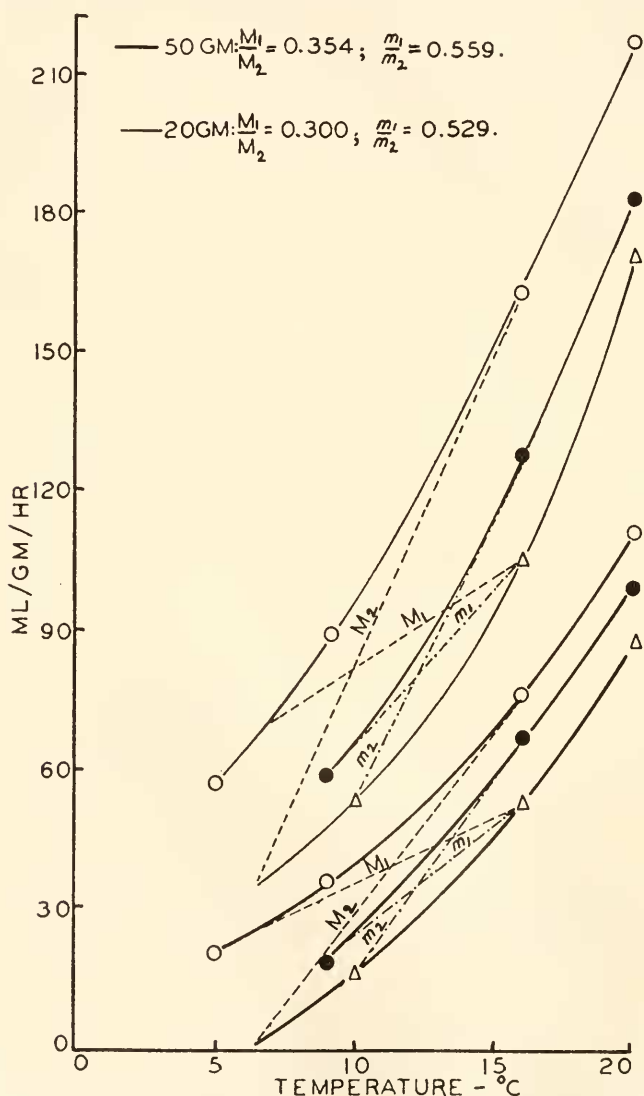


FIGURE 4. Rate of water propulsion as a function of latitude in *Mytilus californianus*. Δ Los Angeles; \bullet Fort Ross; \circ Friday Harbor. Variation of rate in either direction not greater than $\frac{1}{2}\sqrt{n}$, where n is ml./gm./hr.

TABLE I

*Q*₁₀ of rate of water propulsion of *Mytilus californianus* as a function of latitude and size

Latitude	<i>Q</i> ₁₀ (10–20° C.)	
	20 gm.	50 gm.
Los Angeles: 34°00' N	3.2	5.44
Fort Ross: 38°31' N	2.71	3.96
Friday Harbor: 48°27' N	2.36	3.08

shows a higher rate per unit weight at all temperatures compared to an animal weighing 50 gm. from Friday Harbor.

*Q*₁₀ of rate of water propulsion as a function of latitude and size

An examination of the attached table, the results of which are plotted in Figure 5, reveals that over the range of 10–20° C. the *Q*₁₀ for the rate of water propulsion in *M. californianus* increases with increasing weight, while with increasing latitude

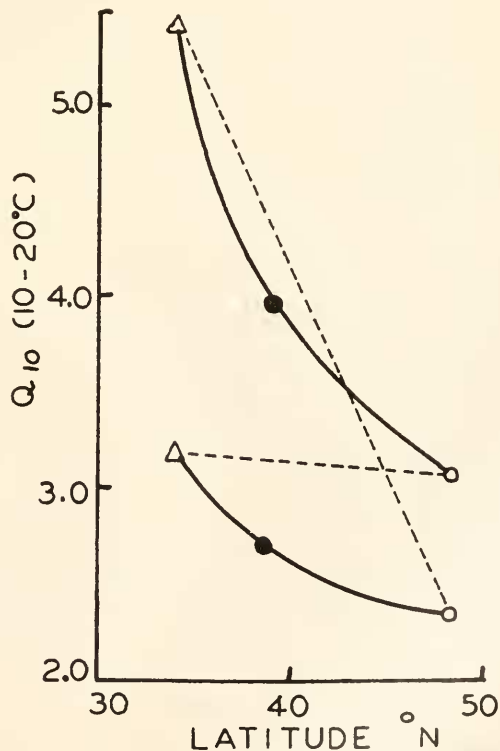


FIGURE 5. *Q*₁₀ as a function of latitude in two different weight groups of *Mytilus californianus*. Bottom curve, 20 gm. individuals; top curve, 50 gm. individuals.

it decreases. Roberts (1952) similarly shows that the Q_{10} for oxygen consumption in *Pachygrapsus crassipes* increases with weight. The change in Q_{10} over the whole range of temperature for each group indicates that the phenomenon reported here is real and is physiologic. Hitherto, it has generally been assumed, chiefly on the basis of the data of Edwards (1946) on insects, that the smaller individuals show greater response to temperature change. A closer examination and analysis of the same data reveal that in *Melanotus* the larger individuals have a slightly higher Q_{10} at all temperatures. Especially marked is the difference at the lower temperatures recorded. The small individuals are not more sensitive to temperature change but have a higher rate at any given temperature, just as in the present case.

This relation between weight and Q_{10} is obviously of the greatest consequence in comparing different weight groups and in the ecology and distribution of poikilotherms.

Temperature compensation coefficient

A comparison of the rates of pumping of mussels of the same weight from different latitudes reveals that *M. californianus* from Friday Harbor has the same rate of pumping at 6.5° C. as the one from Fort Ross at 10° C., while animals from Los Angeles show the same rate at about 12° C. In comparing the degree to which groups of individuals from the same local population acclimatize to high or low temperatures in the laboratory, Roberts (1952) has proposed the ratio between the two slopes, M_1 and M_2 , as a measure of the degree to which acclimatization has been achieved relative to the temperature change and has called it the acclimatization coefficient. M_1 is the slope of the line drawn between the highest temperature rate in the warm-adapted group and the lowest temperature rate in the cold-adapted, while M_2 is just the reverse (Fig. 4: M_1 and M_2 ; m_1 and m_2). This ratio is less than 1 if there is any acclimatization and approaches zero as the degree of acclimatization approaches perfection.

The same procedure may be applied for comparing rates of activity relative to latitudinal difference (assuming this to be chiefly a temperature difference), or, which is the same thing, to express the degree to which animals belonging to the same species located at different latitudes compensate for the temperature change. This may be called the *temperature compensation coefficient*. It cannot be called the acclimatization coefficient because we are dealing with separate populations which may have different genotypes and the term acclimatization should perhaps be reserved for purely phenotypic adaptation.

Interpreting Figure 4 in this light, it is seen that in general smaller animals have lower values for the coefficient, and that the temperature compensation coefficient is lower between Friday Harbor and Los Angeles than between Fort Ross and Los Angeles. In other words smaller animals compensate better than larger animals and more northern mussels show greater compensation to temperature change than those from lower latitudes.

DISCUSSION

That the shell weight is a function of latitude and consequently of the mean annual temperature, is of interest, inasmuch as this morphological feature can be used to determine the physiological nature of a population. The consistency and

small variance of the shell weight also permit its use as an indicator of the temperature of the environment. The relation with the environment may be as close as for the familiar "rules" for vertebrate coloration and proportions.

It is shown that the absolute rate of water propulsion (ml./hr./individual) at minimal habitat temperatures begins to fall after a certain weight is reached, and that this decline is slower in higher latitudes than in lower. The weight-specific rate (ml./hr./gm.), of course, falls with growth and the correlation between the larger size of the northern forms and their relatively slower decrease in activity per gram, plotted against size is similarly significant. Though this does not necessarily imply that the maximal weight to which animals can grow in a given locality can be computed with accuracy by an extrapolation of the available data, still it does show that small differences in temperature are of great significance and that a physiological basis can be found for a well known generalization in ecological geography. This phenomenon of smaller size-dependence of activity in higher latitudes emphasizes a need for obtaining geographically and temporally closely spaced temperature records in inshore waters. The work of Hubbs (1948, 1952) in this direction is noteworthy and is a timely beginning.

In this connection special interest is attached to populations of offshore, deeper water individuals of the same species, particularly of sessile forms like *Mytilus* which have widely dispersed gametes and larvae. If the physiological differences found in populations widely separated latitudinally are based on phenotypic acclimatization, it is to be expected that the same differences will be found between intertidal populations and those at 20 to 30 meters depth, where the temperature is several degrees lower. Adequate material for this comparison has not yet been studied but is available.

The importance of taking weight into consideration when comparing individuals or groups for their activity, especially at various temperatures, is shown not only by the fact that at all temperatures smaller individuals have higher rates as is well known, but by the more significant fact that the Q_{10} as well as the temperature compensation coefficient are lower in smaller individuals. An examination of the data of Fox *et al.* (1936, 1939), already referred to, suggests that almost all the cases in which, at a given temperature, a *higher* rate of activity is reported from *lower* latitudes, are the result of using significantly smaller animals from the lower latitudes. The latter were, in these particular cases, from 2.3 to 45 per cent of the weight of the higher latitudinal animals with which they were compared. Of course the same factor acts to increase the significance of those cases reported where the forms from lower latitude have a *lower* rate at any given temperature, as the authors recognized.

In Figure 5, it may be noticed that the difference in Q_{10} value between a small animal from the north and a larger animal from the south is much greater than that between a small animal from the lower latitudes and a larger animal from the higher latitudes. This means that an organism moving from the northern latitudes toward the lower as it grows must make a tremendously great physiological adjustment as compared to one moving from lower latitudes to the higher. Further, it was observed earlier that amongst the higher latitudinal animals, individuals which are smallest are the first to be affected adversely by raising temperatures. These two facts make it probable that the center of distribution in a species like *Mytilus californianus* lies in the lower latitudes.

The use of the temperature compensation coefficient as a quantitative measure of regulation makes possible analysis and comparison of otherwise not easily comparable physiological phenomena. Shifting an animal from its normal temperatures evokes, in organisms like the mussel, a compensatory response. The degree to which an organism responds and compensates may be related to the degree to which it is removed from its norm. As observed earlier, mussels from more northern latitudes show greater compensation to temperature change than those from intermediate latitudes, not only absolutely but relatively to the temperature difference. Instances which may be parallel are found in human metabolism. Thus, the net efficiency of excess metabolism (over the basal), while walking on level is 20 per cent whereas the net efficiency of excess metabolism, while walking on an 11.4 per cent grade, is 52 per cent (Bazett, 1949). Rothstein and Adolph (1944) found that the amount of voluntary dehydration in acclimatized men is higher, the higher the rate of sweating. Under conditions causing men to sweat less than 400 gms./hr., 95 per cent of the water lost was replaced, whereas men working on the desert and sweating 1000 gms./hr. replaced only 50 per cent of their loss. Gross (1952) reports that regulation against osmotic stress in crabs is greater the greater the stress. The same seems to be true in the regulation of basal metabolism by precise control of heat loss in arctic as compared with tropical mammals and birds (Scholander, *et al.*, 1950). Out of this seems to evolve a principle: the relative compensation for environmental stress increases with increasing departure from a norm, within limits.

SUMMARY

1. Shell weight relative to the weight of soft parts is a constant in any given population of *Mytilus californianus*, but it increases with increasing latitude.

2. The absolute rate as well as weight-specific rate of pumping is greater at any temperature in mussels from higher latitudes than in those of the same weight from lower latitudes.

3. The rate of decline, in the absolute as well as weight-specific rate of pumping, with increasing size, is shown to be slower in higher latitudes than in the lower. This perhaps affords a physiological basis for the larger size of the more northern forms.

4. The Q_{10} of the rate of pumping, between 10 and 20° C., is higher in larger individuals of any given population. But the Q_{10} of individuals of the same weight at different latitudes, shows a decrease with increasing latitude.

5. It is suggested that the center of dispersal of species like *Mytilus californianus* is in the lower latitudes. This suggestion stems from the fact that the difference in Q_{10} values between smaller individuals of lower latitudes and larger individuals of higher latitudes is negligibly small, while the opposite comparison results in a large difference, requiring a great physiological adjustment.

6. A comparison of relative degrees of compensation to temperature at different latitudes is made possible by a proposed temperature compensation coefficient. If the phenomenon under study is a phenotypic change in the lifetime of individuals, this becomes a measure of the degree of acclimatization (Roberts, 1952). This coefficient shows a greater degree of compensation for temperature in more northern samples and in smaller individuals.

7. Such a comparison, and several other instances from earlier work, seem to suggest that the relative compensation to change increases with increasing change.

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